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A new species of *Eliurus* Milne Edwards, 1885 (Rodentia: Nesomyinae) from the Réserve Spéciale d'Ankarana, northern Madagascar

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Abstract. The nesomyine rodent *Eliurus antsingy* is presently known from disjunct limestone regions in the dry lowland forests of northern and western Madagascar. Previous studies of *E. antsingy* noted morphological variation among isolated populations but recognized only a single species. Herein, we examine morphological and genetic variation within and among populations of *E. antsingy* with a particular focus on the taxonomic status of a population from the Réserve Spéciale d'Ankarana in the extreme north of the island. Whereas morphometric analysis cannot distinguish the Ankarana population from its nearest neighbor ~500 km to the south (Namoroka), both are morphologically distinguishable from a population of *E. antsingy* from the type locality (Bemaraha). In contrast, genetic data reveal substantial interpopulation divergence among all three populations, and phylogenetic analysis of these data indicates that the two morphologically similar forms do not form a clade. Based on these results we recognize the population from the Réserve Spéciale d'Ankarana as a new species but given the limitations of current sampling, retain the other two populations as *E. antsingy*.

Keywords. *Eliurus*, Nesomyinae, Rodentia, new species, Ankarana, Madagascar.

1. INTRODUCTION

Of the nine genera of living rodents native to Madagascar (Rodentia: Nesomyidae: Nesomyinae), the genus *Eliurus* Milne Edwards, 1885 is by far the most species-rich. As currently understood, the genus comprises 11 species, five of which have been described since 1994 (Musser & Carleton 2005; Carleton & Goodman 2007). Whereas most of these taxa are known from Madagascar's humid eastern and central forest biomes, two occur in lowland dry forests of the island's western regions. Of these, *E. myoxinus* Milne Edwards, 1885 is a relatively small-bodied form that is broadly distributed throughout western dry forests and into some humid forest areas of the northeast (Soarimalala & Goodman 2003). The second, larger species, *E. antsingy* Carleton, Goodman & Rakotondravony, 2001 has a disjunct distribution and, with the exception of one site, is presently known only from forested habitats that occur on heavily eroded limestone outcroppings known as *tsingy* (Fig. 1). Two specimens of *E. antsingy* were collected in 1964 in the Parc National (PN) de Bemaraha and comprise the holotype and one paratype of this taxon (Carleton et al. 2001). In this same publication, four additional specimens collected from the Réserve Naturelle Intégrale (RNI) de Namoroka in 1999 were also provisionally referred to *E. antsingy*. However, in the course of the description of this taxon, the authors noted that "existing sample sizes of *E. antsingy* are smaller than desirable" and urged "the need for continued study to clarify the interpopulational variation noted" (Carleton et al. 2001, p. 979).

In the time since the original species description of *E. antsingy* was published, additional specimens of a relatively large *Eliurus* were collected from *tsingy* habitats at Ankarana and a nearby zone of metamorphic rock outcrops near Daraina (Fig. 1); these animals were all provisionally assigned to *E. antsingy* (Carleton & Goodman 2007). With the addition of these new records, these authors noted that the "overall amount of craniodental differentiation among the three regions [Bemaraha, Namoroka, and the northern Ankarana + Daraina region] approximates that derived among samples of the broadly distributed *E. majori* [Thomas, 1895]... and they marginally overlap in morphometric space" (Carleton & Goodman 2007, p. 15). This morphometric variation in animals referred to *E. antsingy*, coupled with the disjunct distribution of this species, suggest that these isolated populations might be genetically distinct as well. However, to date no molecular data have been brought to bear on intraspecific differences within this species group. Herein, we examine variation within *E. antsingy* using a combination

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of morphometric and molecular data, with a particular focus on the taxonomic status of the northern populations from Ankarana.

2. MATERIALS AND METHODS

Taxon sampling. Specimens employed in this study are from the following museums: Field Museum of Natural History, Chicago (FMNH); Muséum national d'Histoire naturelle, Paris (MNHN); and Département de Biologie Animale, Université d'Antananarivo, Antananarivo (UADBA). Coordinates used to compose the range map are those given by collectors (see Appendix 1) or those estimated by Carleton et al. (2001).

For our morphometric analyses, we compare specimens from four localities (Fig. 1; see Appendix 1 for specific information on specimens):

A. *Eliurus antsingy* group (Carleton & Goodman 2007)
   1. *Eliurus antsingy* from the Bemaraha formation (FMNH, MNHN, n=3)
   2. *Eliurus antsingy* from the Namoroka formation (FMNH, UADBA, n=14)
   3. *Eliurus antsingy* from the Ankarana formation (FMNH, n=9)

B. *Eliurus majori* group (Carleton & Goodman 2007)
   1. *Eliurus majori* Thomas, 1895, from the montane forests of Montagne d'Ambre (FMNH, n=20). *Eliurus majori* has a broad distribution across the island in montane forest, but the population from Montagne d'Ambre is notably smaller than most other populations of this species. On the basis of body size and geographic proximity, the Montagne d'Ambre population of *E. majori* is the closest to the *E. antsingy* from Ankarana and was therefore included here for comparison.

Morphometric comparisons. We included six external (including mass in g) and 18 craniodental measurements for each specimen. External measurements were obtained from the collectors' original field catalogs or specimen labels and include the following: total length of body and tail (TOTL); head and body length (HBL); length of tail vertebrae (TL); hindfoot length (HFL, excluding claw length except as noted); ear length (EL); and weight (WT). Most of the external measurements were made by the same collector (Goodman).

The 18 craniodental variables (all measured by Goodman) were recorded to 0.1 mm using digital calipers and were based on the measurements defined by Carleton (1994) and include the following: breadth of the braincase (BBC); breadth across both incisive foramina (BIF); breadth of the bony palate across the first upper molars (BM1s); breadth across the occipital condyles (BOC); breadth of the rostrum (BR); breadth of the zygomatic plate (BZP); depth of the auditory bullae (DAB); interorbital breadth (IOB); length of bony palate (LBP); length of diastema (LD); length of incisive foramen (LIF); coronal length of maxillary toothrow (LM1-3); length of rostrum (LR); occipitonasal length (ONL); posterior breadth of the bony palate (PPB); postpalatal length (PPL); width of the first upper molar (WM1); and zygomatic breadth (ZB). We have used Greene (1963), Voss (1988), and Carleton (1994) for the morphological terms and landmarks used herein for craniodental characters.

We sorted all specimens into age categories using qualitative evaluation of tooth wear and the extent of cranial-suture fusion. Specimens with complete but unworn molar rows and an unfused basisphenoid suture were classed as young adults; those with slightly worn molar teeth and a fused basisphenoid suture were considered adults. External measurements from adults were used to establish general size differences between different *Eliurus* populations. Only adult specimens were used in craniodental statistical analyses, which included univariate and multivariate comparisons employing Statistica (version 7.1, series 0306) programs. The latter comparisons included principal component analyses using ln-transformed data and a correlation matrix.

Molecular data. DNA was extracted from 13 animals representing the three populations of *E. antsingy* described above using a DNeasy extraction kit (Qiagen Inc.). The entire cytochrome *b* (cyt-*b*) gene was amplified from genomic DNA using primers MVZ05 and UMMZ04 (see Jansa et al. 1999 for primer sequences). To generate fragments of a suitable size for sequencing, this PCR product was used as a template in two subsequent reamplification reactions, one using primer MVZ05 paired with UMMZ12 and one using UMMZ13 paired with UMMZ04. All PCR reactions were performed using reaction conditions as described in Jansa et al. (2006). All fragments were sequenced in both directions, and resulting sequences have been deposited in GenBank (accession numbers GQ420656-GQ420668).

The resulting cyt-*b* sequences were aligned by eye with reference to translated amino acid sequences. We included additional sequences from *E. majori* from northern (Montagne d'Ambre; FMNH 154610, Genbank Accession AF160552) and southern Madagascar (Midongy-Sud; FMNH 178686, GQ420668), as well as a specimen of *E. danieli* Carleton & Goodman, 2007 (UADBA 10483, AF160553) as outgroups. Phylogenetic analyses were performed using both maximum parsimony (MP) and maximum likelihood (ML) as implemented in PAUP*ver4.0b10 (Swofford 2002). Tree searches using MP were performed using the branch-and-bound algo-

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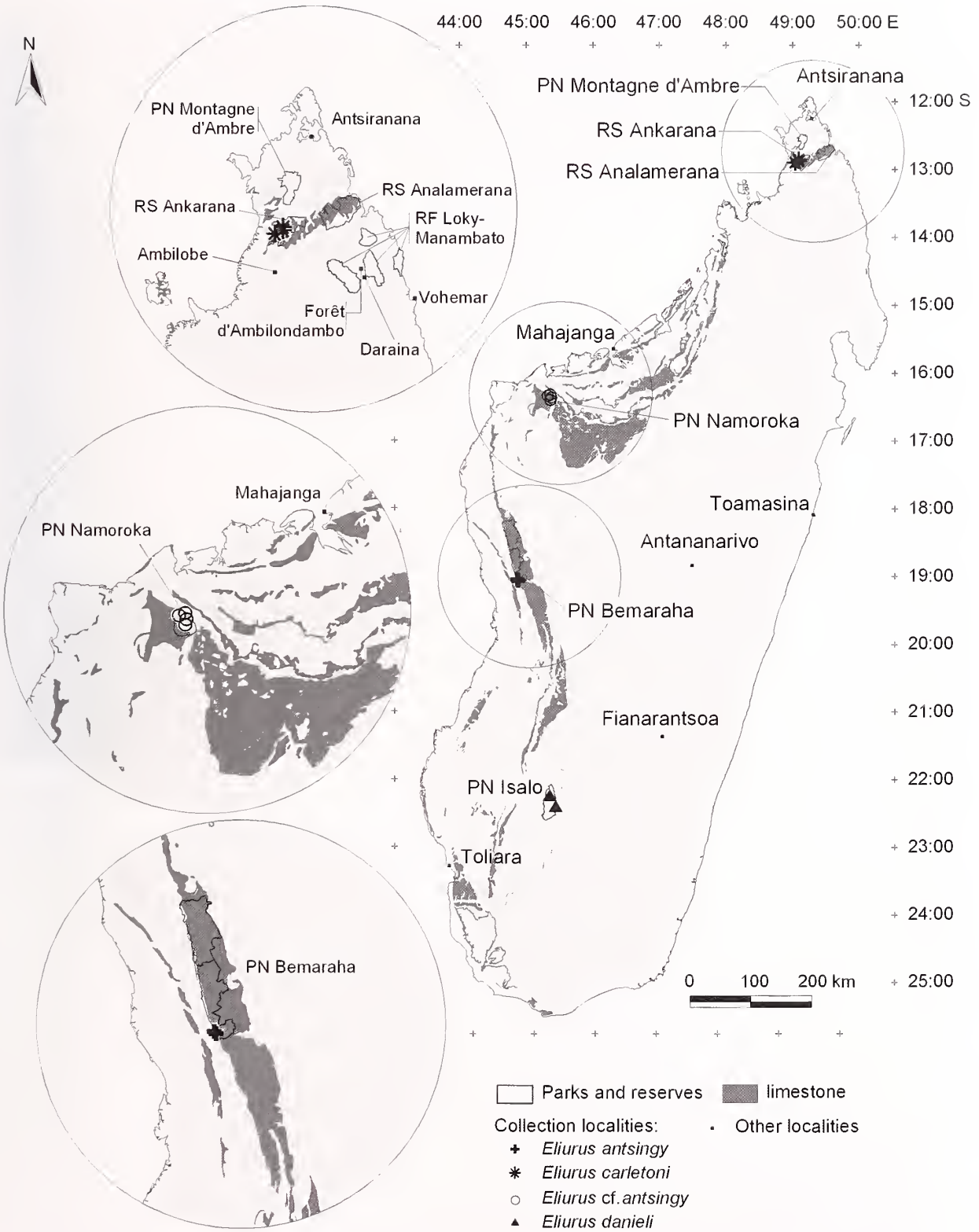

Fig. 1. Map of Madagascar showing localities mentioned in the text. The complete map of the island to the right shows the island wide delineation of limestone deposits based on Bésairie's (1964) classification of the geology of Madagascar. These are extracted from his categories 14 and 18 "Marnes & calcaires" [=marls and chalks]. The three circular areas delineated on the full map are presented in finer detail in the left hand circular insets and in which the distribution of different *Eliurus* spp. are given.

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rithm. For ML analyses, we first identified the best-fit model of nucleotide substitution using the Akaike information criterion (AIC) as employed in ModelTest ver. 3.6 (Posada & Crandall 1998). We subsequently evaluated whether a molecular clock fit our data using a hierarchical log-likelihood ratio test. Parameters for the resulting best-fit model were fixed in a heuristic search using 10 replicates of random taxon addition and TBR branch swapping. Nodal support was calculated for both MP and ML analyses using non-parametric bootstrapping (Felsenstein 1985). All bootstrap analyses employed 1000 pseudoreplicates analyzed with heuristic searches as above. Polymorphism and divergence statistics were calculated using DNAsp ver. 4.10 (Rozas et al. 2003); in addition, we report ML-corrected divergence values as calculated in PAUP*.

3. RESULTS

After comparisons of the specimens from the Réserve Spéciale (RS) d'Ankarana, previously identified as *Eliurus antsingy*, using external and craniodental measurements and characters, as well as a molecular analysis, these animals represent a previously unknown species of Malagasy rodent falling within the *E. antsingy* group (sensu Carleton & Goodman 2007). This new taxon is described below.

Superfamily Muroidea Illiger, 1811

Family Nesomyidae Major, 1897

Subfamily Nesomyinae Major, 1897

Eliurus carletoni, new species
Figs. 2–3; Tables 1–3

Holotype. An adult female specimen in the Field Museum of Natural History (FMNH 173105) prepared as skin, skull, and partial skeleton, collected 9 April 2002 by Steven M. Goodman (original number SMG 12832). The round skin and skull are in fine condition. Recorded external data include: TOTL, 335 mm; HBL, 143 mm; TL, 183 mm; HFL, 29 mm; EL, 25 mm; and WT, 99 gm. The basisphenoid suture is fused and third molar slightly worn. The animal was noted as having large mammae, no embryos or placental scars. The mammae formula was one axial pair and one inguinal pair. Muscle tissue samples were preserved in lysis buffer.

Type locality. Madagascar, Province d'Antsiranana, Réserve Spéciale d'Ankarana, Campement des Anglais (Anilotra), 7.5 km NW Mahamasina, 12°54.4'S, 49°06.6'E; 125 m above sea-level (Fig. 1).

Diagnosis. A species of *Eliurus* falling within the *E. antsingy* species group (sensu Carleton & Goodman 2007) characterized by a dark brown dorsal pelage, contrasting grayish-white venter, unicolor dark brown tail (including terminal tuft), and short hind foot (HFL 28–29 mm) and ears (EL 23–25 mm) (Fig. 2). Cranial size moderately large (ONL 40–41 mm), rostrum relatively short for the genus (LR/ONL ca. 31%), molar rows moderately long (LM1-3 5.4–5.7 mm), incisive foramina notably short and wide (LIF/LD ca. 47–49%), palatine process short and stout, and auditory bullae relatively small in comparison to other members of the *E. antsingy* species group. Given present taxon and character sampling, the species is further diagnosed by the following 18 unreversed synapomorphies in the cyt-*b* gene (the first nucleotide given is the ancestral state, followed by the nucleotide position in the cyt-*b* gene, followed by the derived state. Changes that result in an amino acid replacement are shown in bold;

Fig. 2. Photograph of live *Eliurus carletoni* (FMNH 169718), a young adult male from the forest near the Andrafiabe Cave in the Réserve Spéciale d'Ankarana. The light colored ventral portion of the tail is slightly exaggerated by the photographic flashes. Photograph taken by Harald Schütz.

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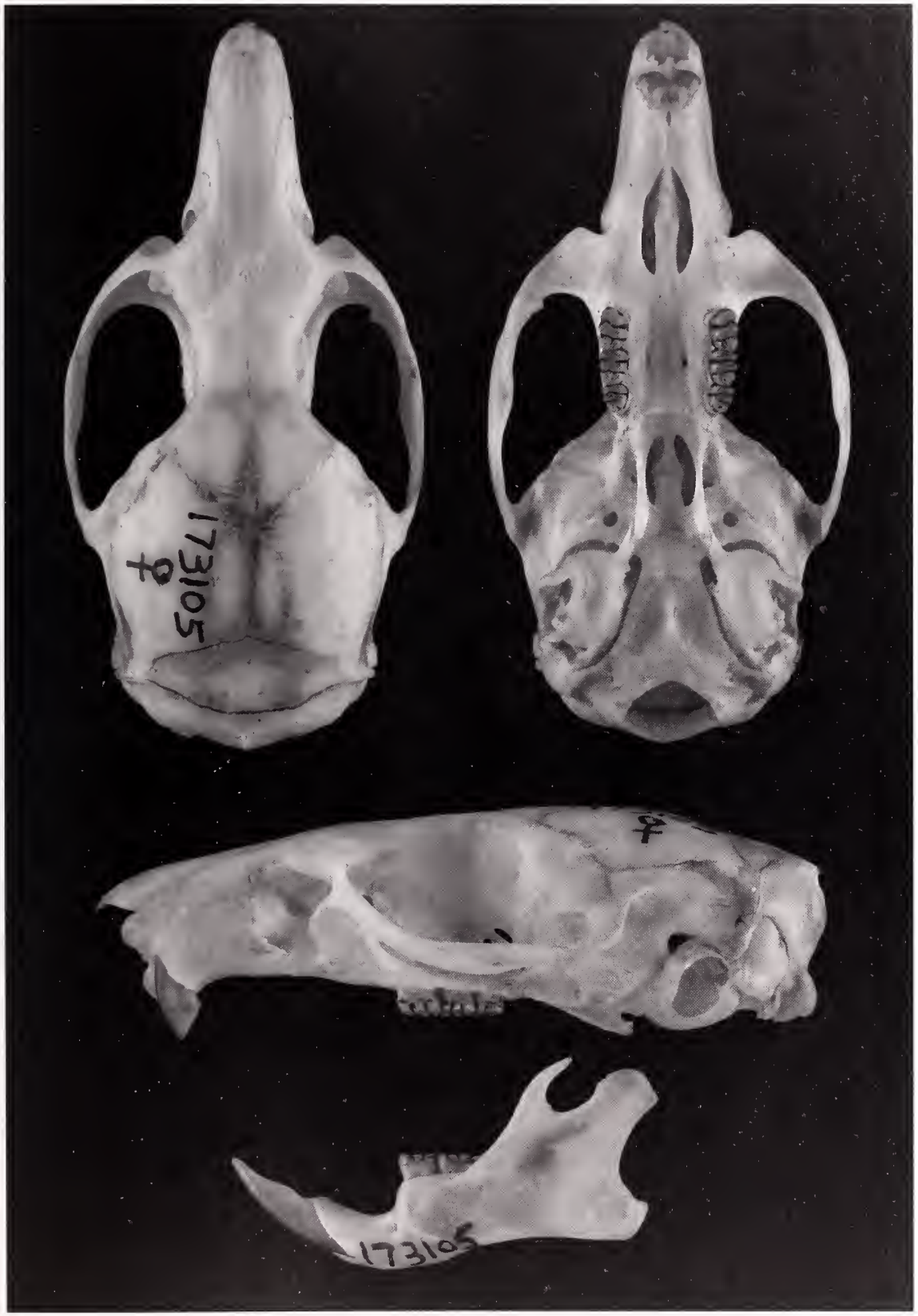

Fig. 3. Different views of *Eliurus carletoni* (holotype FMNH 173105): upper left–dorsal view of cranium, upper right–ventral view of cranium, and lower–lateral view of cranium and mandible. Photograph by John Weinstein (FMNH Z94480_07d).

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Table. 1. Summary statistics (mean ± standard deviation, observed range, and sample size) for external morphological measurements of *Eliurus antsingy* from Bemaraha, *E. antsingy* from Namoroka, *E. carletoni* from Ankarana, *E. danieli* from Isalo, and *E. majori* from Montagne d'Ambre. See Materials and Methods for definitions of acronyms.

Variable	*E. antsingy* Bemaraha	*E. antsingy* Namoroka	*E. carletoni* Ankarana	*E. danieli* Isalo	*E. majori* Montagne d'Ambre
TOTL	354	329.2 ± 21.90 305–364, n=5	328.3 ± 9.07 318–335, n=3	335, 337	336.0 ± 14.62 322–365, n=7
HBL	160	146.8 ± 5.19 142–153, n=4	147.7 ± 4.04 143–150, n=3	150, 152	146.6 ± 4.18 141–154, n=6
TL	186	170.2 ± 15.42 153–195, n=5	174.3 ± 9.61 164–183, n=3	179, 195	179.1 ± 13.66 165–208, n=7
HFL	32	29.8 ± 1.26 28–31, n=4	28.8 ± 0.50 28–29, n=4	30, 32	28.5 ± 1.51 27–31, n=8
EL	26	24.8 ± 1.26 24–25, n=5	24.3 ± 0.96 23–25, n=4	26, 28	19.8 ± 1.49 17–21, n=8
WT	131	92.8 ± 6.55 87–101, n=4	94.8 ± 4.72 88–99, n=4	91, 100	79.5 ± 5.58 70–89, n=8

all other changes are silent): C189T, C201A, C270T, C312T, C321T, C522T, C585A, T598C, T678C, **T710C, C722T**, T768C, T837C, T849C, C879T, A945C, A978G, C1069T.

Referred specimens. Other specimens of *Eliurus carletoni* have been examined in this study, all from the RS d'Ankarana and collected by S. M. Goodman (except as noted). The following three specimens were obtained from the type locality: FMNH 173104 (SMG 12728), a young adult female, with partially fused basisphenoid suture, on 6 April 2002; FMNH 173106 (SMG 12833), a young adult male, with abdominal testes, with unfused basisphenoid suture, on 9 April 2002; FMNH 173109 (SMG 12848), an adult female, with largely fused basisphenoid suture, on 11 April 2002. An additional three specimens were taken from 2.6 km E Andrafiabe, in forest near Andrafiabe Cave, 12°55.9'S, 49°03.4'E; ca. 50 m above sea-level: FMNH 169718 (SMG 11928), a young adult male, with unfused basisphenoid suture, obtained on 22 January 2001; FMNH 169719 (SMG 11946), a young adult female, with unfused basisphenoid suture, on 24 January 2001; FMNH 169720 (SMG 11994), an adult scrotal male, with fused basisphenoid suture, on 26 January 2001. Two additional specimens were collected by Achille P. Raselimanana near the trail junction of routes to Matsaborimanga, Campement des Anglais, and Andafiabe, 10.0 km NW Mahamasina, ca. 12°53.2'S, 49°06.6'E; 100 m above sea-level: FMNH 173107 (SMG 12846), an adult female, with largely fused basisphenoid suture, on 11 April 2002; FMNH 173108 (SMG 12847), a young adult male, with unfused basisphenoid suture, on 11 April 2002. In addition, a number of incomplete cranial specimens referable to *E. carletoni* have been recovered pellets of the Madagascar Red Owl (*Tyto soumagnei*) collected at the RS d'Ankarana, Perte des Rivières (12°57.283'S, 49°7.627'E).

Etymology. This new species is named in honor of Dr. Michael D. Carleton of the National Museum of Natural History, Smithsonian Institution, Washington, D.C. in recognition of his immense contributions to the field of rodent systematics. In particular, Dr. Carleton has worked extensively on the systematics and morphological evolution of Madagascar's native rodents.

Distribution. This species is currently only known from the RS d'Ankarana in the extreme northern portion of Madagascar (Fig. 1). Specimens obtained in the RS d'Analamerana and the Réserve Forestière de Loky-Manambato (Daraina region) may be referable to this taxon; future studies will address this question.

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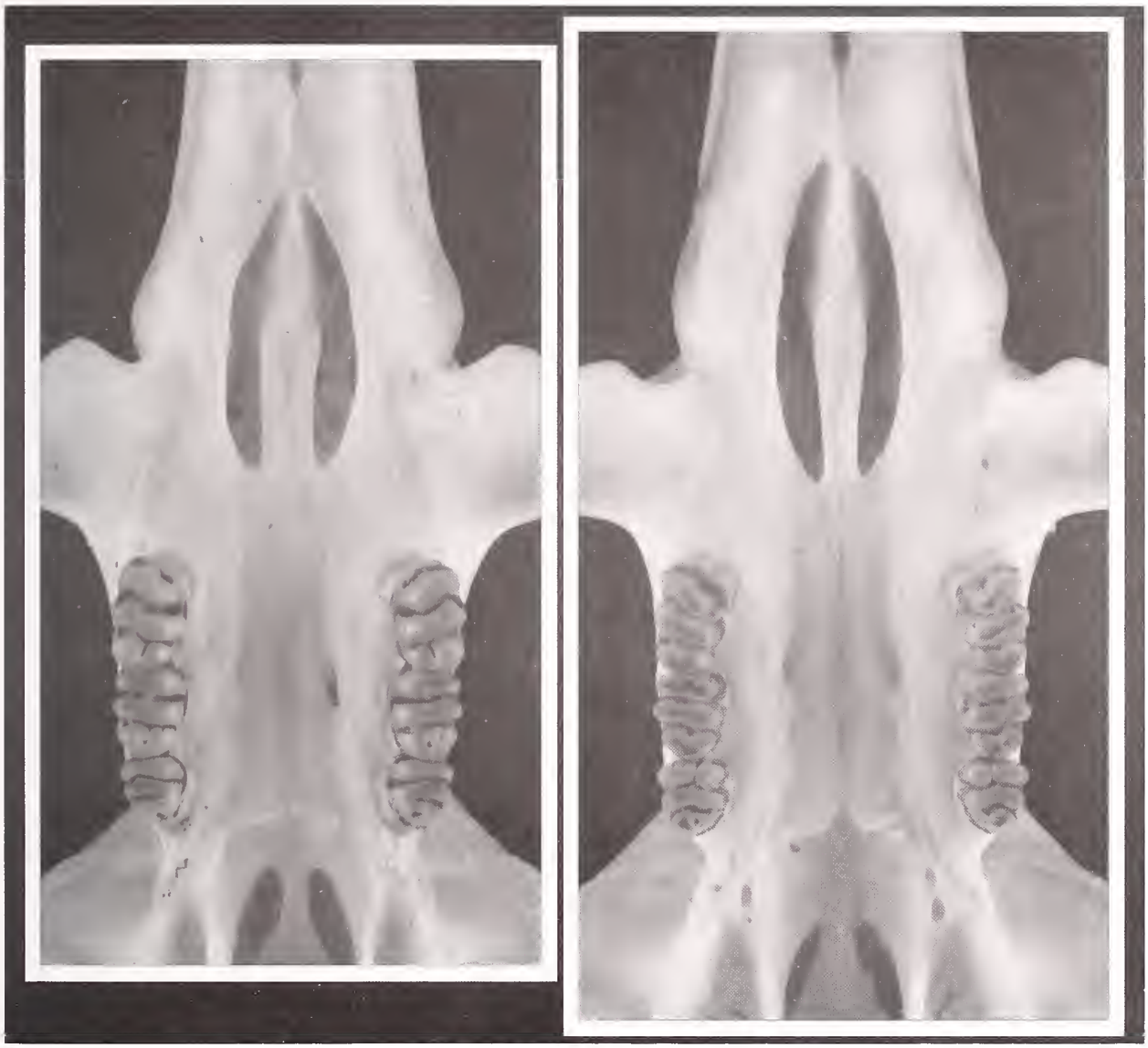

Fig. 4. Comparison of incisive foramen and molar toothrows – (right) in the holotype of *Eliurus carletoni* (FMNH 173105) from the Réserve Spéciale d'Ankarana and (left) *E. antsingy* from the Parc National de Bemaraha (FMNH 172271). Note that this structure is reduced in length and width in the former species, as well as the palatine process, which is thick and short. Photograph by John Weinstein (FMNH Z94480_08d).

Description. Overall body hair texture soft and relatively fine. Dorsum cover hairs 7–9 mm in length over middle rump and 5–6 mm at the level of the nape. Cover hairs of dorsum largely bi-colored with proximal two-thirds dark brown and distal one-third medium buff, although some hairs tipped with faint dusky brown. Guard hairs dark brown to blackish. The overall coloration of the upperparts, including forehead and face, is a dark agouti with a diffused mid-dorsal line that is notably darker than the surrounding fur. In several individuals, this band broadens towards the rump. Fur coloration of lower legs approaches a lighter tannish-brown. In a few individuals (FMNH 173107, 173108), the dorsal pelage coloration is slightly lighter, with the forehead, face, and lower legs being tannish-brown. Along mid-portion of body, the limit between the dorsal and ventral pelage is relatively well demarcated. The coloration of the ventrum is variable and ranges from being nearly entirely white (FMNH 169719, 173107, 173108), being largely white with a diffusion of gray towards the throat and base of limbs (FMNH 173109), to being broadly diffused with light gray and having dusky brown at the base of the limbs (as in holotype FMNH 173105). A diffuse dusky-brown band extends over the mid-portion of the dorsal tarsus surface and prox-

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Table. 2. Summary statistics (mean ± standard deviation, observed range, and sample size) for craniodental measurements of adult *Eliurus antsingy* from Bemaraha, *E. antsingy* from Namoroka, *E. carletoni* from Ankarana, *E. danieli* from Isalo, and *E. majori* from Montagne d'Ambre. See Materials and methods for explanation of acronyms and age classes. Measurements for two of the *E. antsingy* specimens (MNHN 1966.2220, 1966.2222) were taken from Carleton & Goodman (2007).

Variable	*E. antsingy* Bemaraha	*E. antsingy* Namoroka	*E. carletoni* Ankarana	*E. danieli* Isalo	*E. majori* Montagne d'Ambre
ONL	43.2 ± 1.14 41.9–44.1, n=3	41.0 ± 1.40 39.3–42.5, n=5	40.2 ± 0.48 39.5–40.6, n=4	39.1, 40.6	36.9 ± 0.68 36.1–38.0, n=7
ZB	21.2 ± 0.51 20.8–21.8, n=3	19.3 ± 0.62 18.4–20.3, n=6	19.7 ± 0.31 19.4–20.0, n=3	18.9, 19.1	18.8 ± 0.42 18.3–19.4, n=7
BBC	16.1 ± 0.26 15.8–16.3, n=3	15.1 ± 0.20 14.9–15.4, n=6	15.1 ± 0.25 14.8–15.4, n=4	14.6, 15.1	14.4 ± 0.18 14.1–14.7, n=8
IOB	6.1 ± 0.15 5.9–6.2, n=3	5.9 ± 0.14 5.7–6.1, n=6	5.6 ± 0.08 5.5–5.7, n=4	5.3, 5.8	5.2 ± 0.21 4.9–5.5, n=8
LR	14.9 ± 0.21 14.7–15.1, n=3	13.2 ± 0.55 12.7–14.1, n=5	12.6 ± 0.24 12.2–12.7, n=4	12.2, 13.3	11.8 ± 0.37 11.5–12.6, n=7
BR	7.4 ± 0.06 7.4–7.5, n=3	6.8 ± 0.23 6.4–7.0, n=6	7.0 ± 0.17 6.7–7.1, n=4	7.0, 7.4	6.9 ± 0.07 6.8–7.2, n=8
PPL	15.2 ± 0.61 14.7–15.9, n=3	14.3 ± 0.61 13.7–15.0, n=6	14.3 ± 0.25 14.0–14.6, n=4	13.8, 13.8	12.8 ± 0.60 12.0–13.6, n=8
LBP	7.8 ± 0.10 7.7–7.9, n=3	8.1 ± 1.06 7.3–10.2, n=6	7.6 ± 0.21 7.3–7.9, n=4	7.7, 7.8	7.4 ± 0.43 6.8–8.0, n=8
PPB	6.1 ± 0.06 6.0–6.1, n=3	5.5 ± 0.13 5.3–5.6, n=6	5.5 ± 0.22 5.2–5.7, n=4	5.7, 5.9	5.6 ± 0.15 5.4–5.8, n=8
LIF	6.7 ± 0.10 6.6–6.8, n=3	5.7 ± 0.52 4.7–6.0, n=6	5.2 ± 0.22 4.9–5.4, n=4	5.3, 5.4	5.1 ± 0.32 4.6–5.6, n=8
BIF	2.9 ±0.21 2.7–3.1, n=3	2.4 ± 0.22 2.0–2.6, n=6	2.6 ± 0.10 2.4–2.6, n=4	2.7, 2.7	2.2 ± 0.21 2.0–2.5, n=8
LD	11.8 ± 0.56	10.9 ± 0.89	10.7 ± 0.24	9.8, 10.1	9.8 ± 0.21

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Table. 2. (pursuit).

Variable	*E. antsingy* Bemaraha	*E. antsingy* Namoroka	*E. carletoni* Ankarana	*E. danieli* Isalo	*E. majori* Montagne d'Ambre
	11.3–12.4, n=3	10.1–12.5, n=6	10.4–10.9, n=4		9.4–10.0, n=7
BM1s	8.2 ± 0.15 8.0–8.3, n=3	7.5 ± 0.14 7.3–7.7, n=6	7.5 ± 0.26 7.3–7.8, n=4	7.7, 7.7	7.5 ± 0.25 7.0--7.7, n=7
DAB	6.3 ± 0.26 6.0–6.5, n=3	5.7 ± 0.21 5.5–6.0, n=6	5.6 ± 0.17 5.4–5.8, n=4	5.6, 5.8	5.3 ± 0.18 5.0–5.5, n=8
BZP	3.7 ± 0.57 3.2–4.3, n=3	3.9 ± 0.34 3.5–4.5, n=6	3.6 ± 0.15 3.4–3.7, n=4	3.8, 3.8	3.2 ± 0.18 3.0–3.5, n=8
BOC	9.6 ± 0.10 9.5–9.7, n=3	8.8 ± 0.20 8.5–9.1, n=6	8.9 ± 0.17 8.7–9.1, n=4	8.6, 8.7	8.3 ± 0.20 8.1–8.6, n=8
LM1-3	5.8 ± 0.15 5.7–6.0, n=3	5.6 ± 0.23 5.3–5.9, n=6	5.6 ± 0.14 5.4–5.7, n=4	5.9, 6.2	5.9 ± 0.20 5.6–6.3, n=8
WM1	1.6 ± 0.10 1.5–1.7, n=3	1.6 ± 0.08 1.4–1.6, n=6	1.6 ± 0.06 1.5–1.6, n=4	1.6, 1.7	1.7 ± 0.07 1.6–1.8, n=8

imal metatarsus; the balance of these structures is dominated by light-colored fur intermixed with light brown. Relatively well-developed white ungual tufts at base of claws.

Caudal tail tuft prominent over distal half of length, tuft hairs becoming gradually longer toward the tip and measuring about 10–13 mm long near the terminal portion. Tail fur notably mono-colored, dark blackish-brown along complete length. The only exception is FMNH 173108, which has a 7 mm wide largely white-haired section starting about 30 mm from the terminal tip. Proximal half of tail covered with short black hairs that sparsely cover the caudal scales. Ventral tail scales distinctly rectangular-shaped and on the dorsal surface dark brownish and on the ventral surface light gray at base merging to dark brownish distally. One animal with a short bobbed tail (FMNH 169720) has a distorted dark blackish-brown terminal tuft, but there is no evidence of white replacement hair.

Hind feet short and broad; absolutely and relatively smaller than in *E. antsingy* from Bemaraha (FMNH 172721). Plantar pads six and arranged as characteristic of the genus (Carleton 1994, his fig. 2). Pinnae relatively short and not as long as *E. antsingy* from Bemaraha (Table 1); color dark brown externally and sparsely clothed with fine light-colored hairs.

Cranium the size of other moderately large members of the genus (ONL = 39.5–40.6 mm), but more diminutive than *E. antsingy* from Bemaraha (ONL = 41.9–44.1 mm) and smaller on average than *E. antsingy* (ONL = 39.3–42.5 mm) from Namoroka. Similar in overall profile shape to *E. antsingy,* but skull less sharply arched towards occiput (Fig. 3). Rostrum proportionately shorter (LR/ONL = 30.9–31.3%), as compared to *E. antsingy* from Bemaraha (LR/ONL = 34.9%) and all other members of the genus. Braincase not notably rounded as in, for example, *E. danieli* or other members of the *E. majori* group. Subsquamosal fenestra notably reduced, similar to *E. ants-*

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Table. 3. Factor loadings from principal component analyses of log transformed craniodental measurements of specimens of adult *Eliurus antsingy* (Bemaraha and Namoroka), *E. carletoni*, *E. danieli*, and *E. majori* (Montagne d'Ambre). For this analysis, a graphical representation of the first two factors is presented in Fig. 5. On the basis of ANOVA analyses, two craniodental variables, LBP and WM1, showed no significant differences across taxa and were not included in the PCA analysis.

	Factor 1	Factor 2	Factor 3
ONL	-0.944	0.254	0.018
ZB	-0.869	-0.002	-0.048
BBC	-0.939	0.027	0.114
IOB	-0.883	0.215	0.172
LR	-0.944	-0.005	-0.186
BR	-0.457	-0.543	-0.420
PPL	-0.901	0.211	0.119
PPB	-0.602	-0.639	0.0343
LIF	-0.730	-0.472	0.197
BIF	-0.639	-0.421	0.386
LD	-0.831	0.386	-0.214
BM1	-0.618	-0.617	-0.032
DAB	-0.931	0.071	-0.083
BZP	-0.545	0.447	-0.439
BOC	-0.923	-0.125	0.247
LM1-3	0.108	-0.847	-0.254
Eigenvalues	9.842	3.519	1.554
Proportion of total variation explained	54.7%	74.2%	82.9%

ingy from Bemaraha, without exposing the interior braincase. Hamular process of the squamosal reduced and stout, similar to that in *E. antsingy* from Bemaraha. Zygomatic arches not notably heavy, although the zygomatic plates are proportionately stouter as compared to other members of the genus of similar ONL length. Nasolacrimal capsule more inflated and nasolacrimal foramen closer to zygomatic notch than in *E. antsingy* from Bemaraha.

Incisive foramina bluntly pointed on their posterior and anterior ends; notably short (LIF/LD = 47.1–49.5%) for members of the genus; in *E. antsingy* from Bemaraha the LIF/LD = 56% (Fig. 4). Posterior palatine foramina oblong ovals, situated within the maxillary-palatine suture at the level of the M1-M2. Palatine process stout and short. Supernumerary palatal foramina occurring in the palatine bones, but minute in size and irregularly formed: in the holotype these occur on the animal's left side at the level of M2-M3 and on the right side in the central portion of M3. No posterolateral palatal foramen. Posterior margin of the bony palate terminates at the posterior ends of the third molars. The anterior portion of the mesopterygoid fossa is broad, U-shaped, and extending distally without a constriction in the central winged portions of the pterygoid process. Auditory bullae relatively small for the genus; from ventral view the ectotympanic covering only a portion of the petrosal part of auditory bullae and a small portion of the periotic.

Anterior enamel surface of upper and lower incisors dull yellowish-orange. Alveolus of lower incisor terminating at the level of the coronoid process and below the sigmoid notch. The base of the incisor root forming slight rise on mandibular ramus but not a capsular process. Toothrows not particularly elongated (LM1-3 = 5.4–5.7 mm) and relative to cranial size, in proportion to those of *E. myoximus* and *E. tanala* Major, 1896 (Carleton 1994, Appendix 2). Molars robust with trilaminar configuration on planar surface, typical of other members of this genus; upper and lower first and second molars about equal in length and both notably longer than third molars.

Morphological comparisons. On the basis of numerous morphological traits, *E. carletoni* is placed along with *E. antsingy* from Namoroka and Bemaraha in the same species assemblage (Carleton & Goodman, 2007). Given the morphological uniqueness of this species complex, as outline by Carleton et al. (2001) and Carleton & Goodman (2007), our comparisons here are largely confined to other populations within the group. The northern population of *E. majori*, occurring on Montagne d'Ambre, is also included, because this is geographically the closest known moderately sized *Eliurus*. Further comparisons are also made to *E. danieli* from transitional dry/humid forests of the PN de l'Isalo in the central west. Both *E. majori* and *E. danieli* are included within the *E. majori* group, which Carleton & Goodman (2007) allied with the *E. antsingy* group (see below).

In general, the dorsal pelage coloration of *E. carletoni* is similar to *E. antsingy*; however, the dorsum cover hairs towards the middle rump tend to be slightly longer in *E. antsingy* (9–11 mm) as compared to *E. carletoni* (7–9 mm). Specimens of *E. majori* from Montagne d'Ambre have distinctly dark slate gray dorsums and a denser and more svelte dorsal pelage and those of *E. danieli* have bright plumbeous gray cover hairs. The ventral pelage of *E. carletoni* varies from only being slightly tinged with white in FMNH 173105 (the holotype), to being largely white-bellied. However, in all cases *E. carletoni* has more

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whitish-colored fur on the belly than *E. antsingy* from Bemaraha (FMNH 172721), whereas all eight of the skin preparations of *E. antsingy* from Namoroka have white venters. Both *E. carletoni* and *E. antsingy* have mono-colored tails, generally with dark-blackish brown fur along the complete length, and the caudal tuft occupies the distal half of the tail. Some individuals of *E. antsingy* from Namoroka have notably light brown tails and reduced caudal tufts; these include both young adults (FMNH 178591, 178593) and full adults (FMNH 178592) and this difference does not appear to be age related. Amongst the specimens of *E. carletoni* there is one anomalous case (FMNH 169720), which has a small white band along its length. Other species of *Eliurus* with largely mono-colored dark-blackish brown tails include *E. myoxinus* and *E. webbi* Ellerman, 1949, which can be distinguished from *E. carletoni* by the tail length and pilosity, as well as numerous craniodental characters (Carleton 1994, 2003; Carleton et al. 2001).

Eliurus carletoni is distinctly smaller and lighter than *E. antsingy* from Bemaraha (FMNH 172271), but overlaps in all external measurements with specimens of *E. antsingy* from Namoroka (Table 1). The cranium of *E. carletoni* (ONL = 39.5–40.6 mm) approximates the size of other moderately large members of the genus (Carleton 1994), including *E. danieli* and *E. majori,* but it is notably smaller than *E. antsingy* from Bemaraha (ONL = 41.9–44.1 mm) and smaller on average than *E. antsingy* (ONL = 39.2–42.5 mm) from Namoroka (Table 2). The rostrum is proportionately shorter in *E. carletoni* (LR/ONL = 30.9–31.3%) as compared to *E. antsingy* from Bemaraha (LR/ONL = 34.2–35.1%) and from Namoroka (LR/ONL = 32.3–33.2%), as well as most other members of the genus (calculated from descriptive statistics in Carleton, 1994, Appendix 2): *E. minor* (LR/ONL = 33.3%), *E. myoxinus* (LR/ONL = 34.1%), *E. majori* (LR/ONL = 34.4%), *E. tanala* (LR/ONL = 36.0%), *E. webbi* (LR/ONL = 35.3%), and *E. petteri* Carleton, 1994 (LR/ONL = 35.3%).

The hamular process of the squamosal notably reduced within the *E. antsingy* group; in contrast to *E. danieli* and *E. majori* (from Montagne d'Ambre) in which the hamular process is elongated and associated with a more prominent subsquamosal foramen. *Eliurus carletoni* has a notably short (LIF/LD = 47.1–49.5%) and bluntly pointed incisive foramen, as compared to *E. antsingy* from Bemaraha (LIF/LD = 56%; Fig. 4). The palatine process in *E. carletoni* is generally thick and short, particularly in

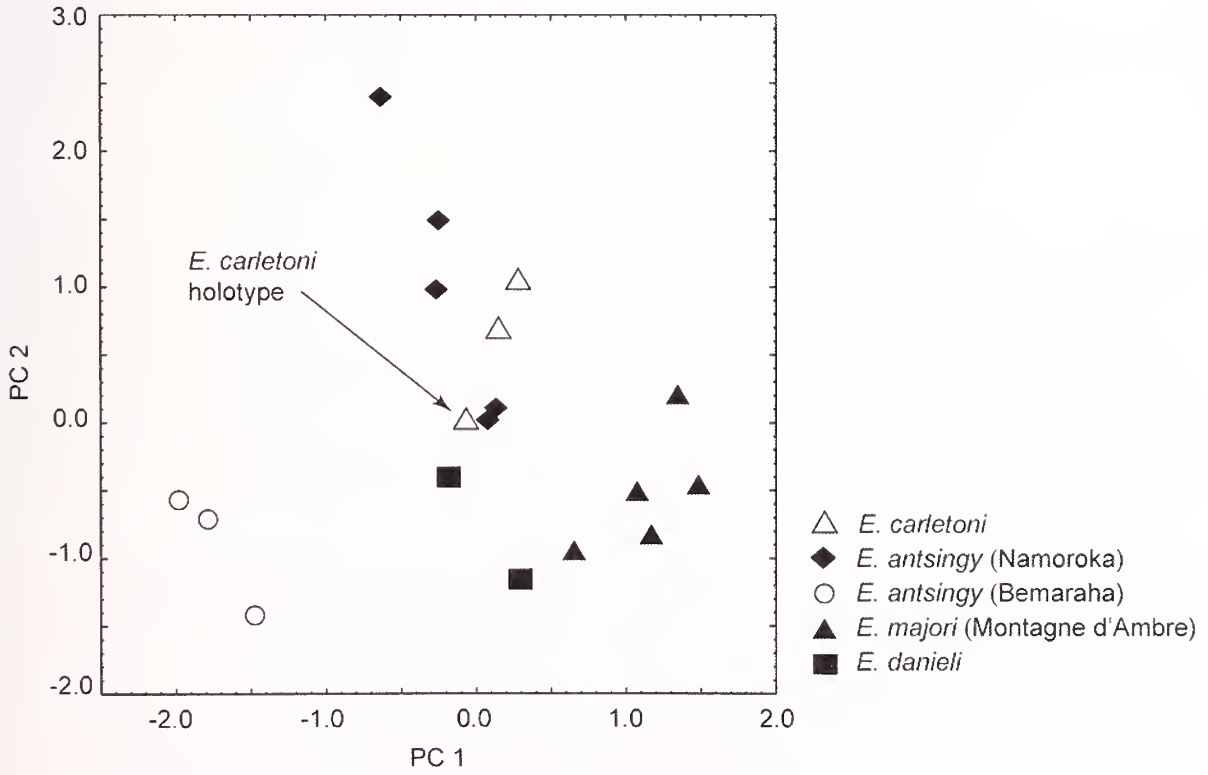

Fig. 5. Projections of factor 1 (x-axis) and factor 2 (y-axis) in principal component analysis on 16 ln-transformed craniodental variables of *Eliurus* spp. Loadings of variables on each axis are shown in Table 3.

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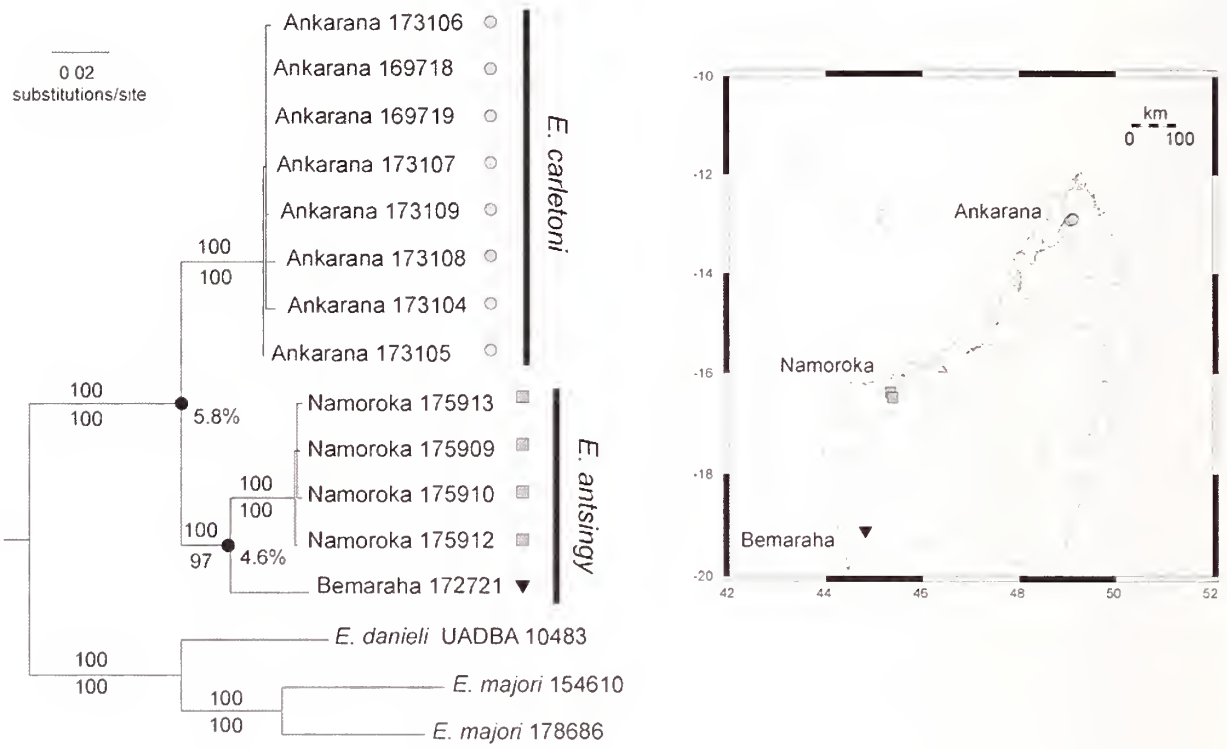

Fig. 6. The maximum-likelihood phylogeny inferred from analysis under the best-fit model of nucleotide substitution for the cyt-*b* data (GTR + I, no clock; -lnL = 3137.31). The tree is rooted with sequences of *Eliurus danieli* and two *E. majori*. The ingroup consists of specimens referred to *E. antsingy* or *E. carletoni*. Terminal branches within the ingroup are labeled with collecting localities shown in the map (right), followed by the museum (FMNH, unless otherwise noted) voucher number. Numbers above and below branches refer to maximum-likelihood and parsimony bootstrap support, respectively. The divergence between populations (ML-corrected) is shown next to circles at each interpopulation node.

comparison to the narrow and relatively long structure in *E. antsingy* and members of the *E. majori* group. The posterior palatine foramina are consistently the same size and are positioned within the maxillary-palatine suture at the level of the M1-M2 for all members of the *E. majori* and *E. antsingy* groups. The external portion of the auditory bullae of *E. carletoni* is notably smaller than in *E. antsingy* from Bemaraha (DAB 5.4–5.8 mm vs. 6.0–6.5 mm), whereas animals from Namoroka largely overlap *E. carletoni* in this measurement (DAB 5.5–6.0 mm).

In all specimens of *E. antsingy* and *E. carletoni*, the molars have a robust trilaminar configuration and the anterior enamel surface of upper and lower incisors are dull yellowish-orange. The position of the lower incisor root with respect to the coronoid process is likewise consistent across members of this group. The toothrows in *E. carletoni* are shorter than *E. antsingy* from Bemaraha (LM1-3 = 5.4–5.7 mm vs. 5.7–6.0 mm), but overlap with those in specimens from Namoroka (LM1-3 = 5.3–5.9 mm). Members of the *E. antsingy* group have proportionately shorter molar rows relative to cranial size than members of the *E. majori* group: *E. carletoni* LM1-3/ONL = 13.7–14.0%, *E. antsingy* from Bemaraha LM1-3/ONL = 13.6%, *E. danieli* LM1-3/ONL = 15.1–15.3%, and *E. majori* from Montagne d'Ambre LM1-3/ONL = 15.5–16.6%. Members of the *E. antsingy* species assemblage have the upper and lower third molars subequal in length to the first and second molars. The same condition is found in *E. danieli*, while the three molars are largely the same size in *E. majori* from Montagne d'Ambre.

Principal Component Analysis of craniodental measurements (Fig. 5) shows complete separation of *E. antsingy* taken in Bemaraha from *E. carletoni* and *E. majori* from Montagne d'Ambre; although there is broad overlap between *E. carletoni* and *E. antsingy* from Namoroka. The factor loadings for this analyses (Table 3) indicates that the majority of variables for factor 1 and coronal length of maxillary toothrow (LM1-3) for factor 2 showed heavy negative loadings. Factor 1 explained 54.7% of the total variation, factor 2 an additional 19.5%, and factor 3 an-

Table. 4. Unreversed synapomorphies (inferred from parsimony optimization on the tree shown in Fig. 6) from the cyt-*b* gene that diagnose *Eliurus carletoni, E. antsingy,* and populations of *E. antsingy* from Namoroka and Bemaraha.

	E. carletoni			***E. antsingy* (Namoroka + Bemaraha)**			
Character No.	Change	Codon position	Effect	Character No.	Change	Codon position	Effect
189	C→T	3	silent	45	C→T	3	silent
201	C→A	3	silent	120	C→T	3	silent
270	C→T	3	silent	243	T→C	3	silent
312	C→T	3	silent	315	T→C	3	silent
321	C→T	3	silent	438	T→C	3	silent
522	C→T	3	silent	567	T→C	3	silent
585	C→A	3	silent	591	A→G	3	silent
598	T→C	1	silent	696	C→A	3	silent
678	T→C	3	silent	715	C→T	1	silent
710	T→C	2	Met→Thr	798	C→T	3	silent
722	C→T	2	Ser→Phe	894	T→C	3	silent
768	T→C	3	silent	906	C→T	3	silent
837	T→C	3	silent	963	T→C	3	silent
849	T→C	3	silent	969	A→G	3	silent
879	C→T	3	silent	1038	C→T	3	silent
945	A→C	3	silent	1083	T→C	3	silent
978	A→G	3	silent				
1069	C→T	1	silent				
	***E. antsingy* (Namoroka)**			***E. antsingy* (Bemaraha)**			
Character No.	Change	Codon position	Effect	Character No.	Change	Codon position	Effect
67	A→G	1	Thr→Ala	48	C→A	3	Asn→Lys
138	C→T	3	silent	108	C→A	3	silent
198	C→T	3	silent	207	T→C	3	silent
201	C→T	3	silent	273	C→T	3	silent
240	C→T	3	silent	279	C→T	3	silent
280	T→C	1	silent	303	A→T	3	silent
364	A→G	1	Thr→Ala	345	A→G	3	silent
426	G→A	3	silent	369	A→G	3	silent
471	A→G	3	silent	396	A→G	3	silent
489	A→G	3	silent	528	C→T	3	silent
582	A→G	3	silent	585	C→T	3	silent
621	C→T	3	silent	654	C→T	3	silent
630	C→T	3	silent	687	C→T	3	silent
999	C→T	3	silent	724	C→T	1	silent
1068	C→T	3	silent	831	T→C	3	silent
1095	T→C	3	silent	1078	G→A	1	Ala→Thr
1122	C→T	3	silent	1093	T→C	1	Phe→Leu
				1124	A→G	2	Asn→Ser
				1138	A→G	1	Asn→Asp

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other 8.7%. Whereas it is the case that *E. carletoni* and *E. antsingy* from Namoroka showed broad morphological overlap in the PCA, based on the molecular phylogeny (see next section) these two populations are not sister taxa within the *E. antsingy* species group.

Molecular variation and phylogeny. There were 6 unique cyt-*b* haplotypes among the 8 specimens from Ankarana, and nucleotide diversity (π) among them was 0.003. Each of the specimens from the Namoroka population had a unique haplotype, and nucleotide diversity within this population was also 0.003. Average sequence divergence (corrected for within-population polymorphism; Nei 1987, eq. 10–21) was 4.4% (ML-corrected divergence = 4.6%) between the Namoroka and Bemaraha populations and 4.9% (5.8% ML-corrected) between Ankarana and the two southern populations.

Phylogenetic analysis of the cyt-*b* dataset using parsimony resulted in three minimum-length trees (L = 350; CI = 0.80; RI = 0.86). The strict-consensus of these trees is less resolved than but entirely consistent with the topology resulting from a maximum-likelihood analysis of this dataset under its best-fit model (GTR+I, no clock; Fig. 6). Two well-supported clades are apparent within *E. antsingy* when this tree is rooted with *E. danieli* and two individuals of *E. majori*. The first includes the specimens from Ankarana, the second comprises specimens from Namoroka and Bemaraha. When character state changes are optimized on this phylogeny, 18 unreversed synapomorphies can be mapped to the branch subtending the Ankarana specimens (*E. carletoni*); two of these result in amino acid substitutions. An additional 16 unreversed synapomorphies (all silent changes) can be mapped to the branch subtending *E. antsingy* from Namoroka and Bemaraha (Table 4).

Ecological notes. All of the specimens of *E. carletoni* used in this study were collected in the forests of the Ankarana Massif, specifically the RS d'Ankarana in northern Madagascar (Fig. 1). This region lies on a block of karstic limestone that was formed during the Jurassic and subsequently uplifted (Cardiff & Befourouack 2003). The weathering of the exposed limestone surface has formed the pinnacle karst known in Malagasy as *tsingy*, which is characteristic of the Ankarana Massif, as well as the *tsingy* habitat at Bemaraha and Namoroka.

The zone surrounding the Ankarana Massif receives slightly less than 2000 mm of rainfall annually, of which most falls between the months of December to April, resulting in a prominent seven-month dry season (Fowler et al. 1989; Hawkins et al. 1990). The deep canyons, which provide protection from the sun and desiccating wind, and underground streams passing close to or resurging at ground level, result in relatively mesic forest conditions within these formations. It is in such areas that *E. carletoni* has been found during biological inventories.

On the basis of trap captures set both on the ground and along lianas, *E. carletoni* can be characterized as a primarily scansorial forest-dwelling inhabitant of the dry deciduous habitats of the Ankarana Massif. It has been trapped in pristine and disturbed forests, generally associated with *tsingy* rock formations, and on the ground, branches and vines. Some notes associated with captured animals help to characterize the different microhabitats it occupies: "...at base of *tsingy*. Trap on ground between rocks and just above water source" (FMNH 169718); "at base of *tsingy*. Trap 1.75 m off ground on 5 cm diam[eter] liana arching over ground to mid-canopy" (FMNH 169719); "Trap on ground in narrow passage between two rocks – resting on *tsingy*" (FMNH 169720); "Trap on ground along large fallen and rotten tree trunk next to *tsingy* wall" (FMNH 173104); "Trap about 1 m off the ground on 20 cm diam[eter] fallen tree trunk" (FMNH 173106); and "In disturbed deciduous forest. Not within 500 m of *tsingy* formation" (FMNH 173107, 173108).

On the basis of rapid inventory information it is difficult to infer many details on the reproductive behavior and seasonality of *E. carletoni*, but a few observations can be presented. Individuals collected in late January 2001 included a young adult male and a female (FMNH 169718, 169719) that were not in reproductive condition, as well as an adult male (FMNH 169720) with large scrotal testes and convoluted epididymides. A series of animals captured during early April 2002 included one adult male that was not in reproductive condition (FMNH 173106); three females each of which had large mammae but no embryos, and one of which had discernable placental scars (one in each the left and right uterine horns) (FMNH 173104, 173107, 173109); and a male with partially scrotal testes, (measuring 5 x 5 mm) and slightly convoluted epididymides (FMNH 173108).

A recent study on the dietary habits of the owl *Tyto soumagnei* within the RS d'Ankarana, found that this raptor feeds extensively on *E. carletoni* (which was identified as *E. antsingy* in that study). Across several different seasons and years, *E. carletoni* comprised 22.1% of the minimum number of individuals and 49.8% of the biomass consumed by this owl (Cardiff & Goodman 2008). At Ankarana, other than the bat fauna (14 species; Goodman et al. 2005), the diversity of mammals weighing less than 100 gm is rather limited. No other species of native rodent has been captured at this site, but two species of introduced rodent (*Rattus rattus* [Linnaeus, 1758] and *Mus musculus* Linnaeus, 1758) occur here. In addition, a shrew (*Suncus madagascariensis* [Coquerel, 1848]), a small

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shrew-tenrec (*Microgale brevicaudata* G. Grandidier, 1899), and a mouse lemur (*Microcebus tavaratra* Rasoloarison, Goodman & Ganzhorn, 2000) are known from the reserve. Previous reports of *E. myoxinus* in Ankarana (Nicoll & Langrand 1989) have not been substantiated during recent biological inventories (Carleton et al. 2001; Goodman, unpublished data).

4. DISCUSSION

Carleton & Goodman (2007) examined morphological variation in described members of the genus *Eliurus* and divided these animals into five different groups. Two of the species assemblages important for the current discussion include the *Eliurus majori* group (comprising *E. majori*, *E. penicillatus* Thomas, 1908, and *E. danieli*) and the *Eliurus antsingy* group (comprising *E. antsingy*, and the newly described *E. carletoni* presented herein). On the basis of several external morphological and craniodental characteristics, these authors suggested that these two species groups might be more closely related to each other than either is to any other species of *Eliurus*. This hypothesis remains to be critically tested with molecular data, but preliminary results based on mitochondrial cyt-*b* data (Jansa, unpublished data) lend credence to this suggestion.

As currently understood, members of the *E. antsingy* group have a broad but disjunct geographic distribution across northern Madagascar, and occur in zones of lowland deciduous forest resting on limestone outcrops (Fig. 1). The type locality of *E. antsingy* is the Bemaraha Plateau in central west Madagascar, a limestone formation dating from the mid-Jurassic. In their description of this taxon, Carleton et al. (2001) tentatively assigned *Eliurus* specimens from the Namoroka Massif – another *tsingy* limestone area 300 km further to the north – to *E. antsingy*. However, they noted that the animals from Namoroka were consistently smaller and had whiter ventral pelage than those from Bemaraha; these differences are upheld in the larger sample from Namoroka presented herein. Based on our molecular phylogeny of the *E. antsingy* species group (Fig. 6), the Namoroka animals are the sister taxon of the animal from Bemaraha, but the two populations differ by an average of 4.7% (ML-corrected) sequence divergence, and there are several fixed changes in the cyt-*b* gene that uniquely characterize each (Table 4). Therefore, these two populations could be considered two distinct species, or they may simply represent extremes of variation in a contiguous population. Our Bemaraha samples of *E. antsingy* come from the southern end of this approximately 100 km limestone formation and additional material from the unsampled *tsingy* habitat in the northern portion of this formation could harbor populations that will be critical for assessing the species status of the Bemaraha and Namoroka populations, which are here conservatively retain as the single species *E. antsingy*.

The *Eliurus* specimens from the Ankarana Massif – described here as *E. carletoni* – as well as a large-bodied *Eliurus* from the Forêt d'Ambilondambo (Daraina) were collected after Carleton et al. (2001) published their description of *E. antsingy*. Carleton & Goodman (2007) tentatively assigned these specimens to *E. antsingy* based on morphometric comparisons, but they called for additional collections from intermediate localities as well as genetic data to test this conclusion. Although we lack critical specimens from new locales, the application of molecular data to existing specimens clearly shows that the Ankarana population is reciprocally monophyletic relative to *E. antsingy* from Namoroka and Bemaraha, and that the two clades differ by 5.8% (ML-corrected) sequence divergence. In addition, the two species are diagnosable by several fixed changes in the cyt-*b* gene (Table 4). Additional collections from limestone areas – such as Ankara and Kelifely – between Namoroka and the northern portion of the island will help to resolve whether these two populations are genetically isolated. However, the lack of gene flow and high degree of molecular divergence between them apparent in this study, leads us to recognize the Ankarana population as a new species, *E. carletoni*. We note that specimens from Daraina are morphologically very similar to *E. carletoni* and may be assignable to this species as well. Ongoing morphological and molecular studies will help resolve this as well as other pressing questions in *Eliurus* systematics.

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Zusammenfassung. Die Nager-Art *Eliurus antsingy* (Nesomyinae) ist aktuell aus einigen disjunkten Kalkstein-Regionen in trockenen Tiefland-Waldgebieten im nördlichen und westlichen Madagaskar bekannt. Frühere Untersuchungen haben morphologische Unterschiede zwischen Individuen aus verschiedenen isolierten Populationen festgestellt, sahen aber alle als Angehörige derselben Art an. In der vorliegenden Untersuchung über-

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prüfen wir die morphologische und genetische Variabilität innerhalb von und zwischen Populationen von *E. antsingy*, mit Schwerpunkt auf dem Status der Population der Réserve Spéciale d'Ankarana im äußersten Norden der Insel. Während eine Unterscheidung der Population in Ankarana von der ihr nächst vorkommenden ~500 km südlich (Namoroka) nicht möglich ist, unterscheiden sich beide Populationen in morphologischen Merkmalen von der der Typuslokalität (Bemaraha) der Art. Im Gegensatz dazu bestehen zwischen allen drei Populationen deutliche genetische Unterschiede. Die phylogenetische Analyse dieser Daten deutet darauf hin, dass die beiden morphologisch ähnlichen Formen keine Schwester-Taxa sind. Auf der Grundlage dieser Ergebnisse sehen wir die Tiere der Réserve Spéciale d'Ankarana als neue Art an, fassen aber diejenigen aus den beiden anderen untersuchten Populationen wegen nicht ausreichend großer Stichproben vorläufig weiterhin als *E. antsingy* auf.

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APPENDIX

Specimens Examined of *Eliurus*

Listed below are specimens that formed the basis for the study's morphological comparisons. FMNH numbers in bold indicate specimens also used in the molecular study. Abbreviations for protected areas in Madagascar are: PN, Parc National; RNI, Réserve Naturelle Intégrale; RS, Réserve Spéciale.

Eliurus antsingy: Mahajanga Province: Antsingy forest near Bekopaka, ca. 19°07.5'S, 44°49.0'E (MNHN 1966.2220, 1966.2222); PN de Bemaraha, 3.5 km E Bekopaka, near Tombeau Vazimba, 100 m, 19°08.4'S, 44°49.7'E (FMNH **172721**); RNI [now PN] de Namoroka (FMNH 167563-167566; UADBA 16169); RNI [now PN] de Namoroka, 26 km NW Andranomavo, Forêt d'Ambovonomby, 200 m, 16°28.2'S, 45°20.9?E (FMNH **175909**, **175910**, 175911); RNI [now PN] de Namoroka, 31 km NW Andranomavo, Forêt de Mahabo, 100 m, 16°23.4'S, 45°20.9'E (FMNH **175912**, **175913**); RNI [now PN] de Namoroka, Site Andriabe, 2.0 km SE Namoroka (village), 16°24.4'S, 45°18.4'E, 110 m (FMNH 178587, 178591-178593).

Eliurus carletoni: Antsiranana Province: RS d'Ankarana, 2.6 km E Andrafiabe, forest near Andrafiabe Cave, 50 m, 12°55.9'S, 49°03.4'E (FMNH **169718**, **169719**, 169720); RS d'Ankarana, Campement des Anglais (Anilotra), 7.5 km NW Mahamasina, 125 m, 12°54.5'S, 49°06.6'E (FMNH **173104**, **173105**, **173106**, **173109**); RS d'Ankarana, 10 km NW Mahamasina, 100 m, 12°53.2'S, 49°06.6'E (FMNH **173107**, **173108**).

Eliurus danieli: Fianarantsoa Province: PN de l'Isalo, 28 km SE Berenty-Betsileo, along Sahanafa River near foot of Bevato Mountain, 22°19.0'S, 45°17.6'E, 650 m (FMNH 175934, UADBA **10483**); PN de l'Isalo, 24 km W Ranohira bas, Andranohavo (Canyon des Rats), 22°28.9'S, 45°22.9'E, 700 m (FMNH 175933).

Eliurus majori: Antsiranana Province: PN de Montagne d'Ambre, 12 km SW Joffreville, Grand Lac, 1325 m, 12°35.8'S, 49°09.6'E (FMNH 154345); PN de Montagne d'Ambre, 5.5 km SW Joffreville, 1000 m, 12°31.6'S, 49°10.3'E (FMNH 156341-156344, 154603-154609, **154610**, 154611-154616). Province de Fianarantsoa : PN de Midongy-Sud, NE slope Mt Papango, 3.5 km SW Befotaka, 1100–1450 m, 23°50.3'S, 46°57.5'E (FMNH **178686**).

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